

The earliest Mesopsychidae and revision of the family Mesopanorpodidae (Mecoptera)

Alexei S. Bashkuev

Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, 117997, Russia

urn:lsid:zoobank.org:author:CC364585-B8BB-4C0D-A612-D64EE9C6548B

Corresponding author: *Alexei S. Bashkuev* (fossilmec@gmail.com)

Academic editor: *D. Shcherbakov* | Received 26 May 2011 | Accepted 25 July 2011 | Published 24 September 2011

urn:lsid:zoobank.org:pub:8D6B3452-50A8-4575-B49B-E83BE378CA3C

Citation: Bashkuev AS (2011) The earliest Mesopsychidae and revision of the family Mesopanorpodidae (Mecoptera). In: Shcherbakov DE, Engel MS, Sharkey MJ (Eds) *Advances in the Systematics of Fossil and Modern Insects: Honouring Alexandr Rasnitsyn*. ZooKeys 130: 263–279. doi: 10.3897/zookeys.130.1611

Abstract

The family Mesopanorpodidae is revised. Most taxa referred to this family are not related to the type genus *Mesopanorpodes* Tillyard, 1918. The type species of the latter, *Mesopanorpodes wianamattensis*, is closely related to *Mesopsyche* Tillyard, 1917. Therefore *Mesopanorpodes* is transferred to Mesopsychidae Tillyard, 1917 (= Mesopanorpodidae Tillyard, 1918, **syn. n.**). The earliest Mesopsychidae are described from the Upper Permian of European Russia (Severodvinsk; Isady locality, Vologda Province): *Permopsyche issadensis* **gen. et sp. n.** (type species) and *P. rasnitsyni* **sp. n.** Two species described under *Mesopanorpodes* from the Upper Permian of Australia are also included into *Permopsyche*: *P. belmontensis* (Riek, 1953), **comb. n.**, *P. robustus* (Riek, 1953) **comb. n.** The first pre-Triassic *Mesopsyche*, *M. incompleta* **sp. n.** is described from the uppermost Permian (the town of Vyazniki, Vladimir Province). *Bittacopanorpa javorskii* Zalesky, 1935 from the uppermost Permian or basal Triassic of Kuznetsk Basin is identified as a hindwing of *Mesopsyche*: *M. javorskii* (Zalesky, 1935) **comb. n.** The origin, evolutionary history, and stratigraphic occurrence of Mesopsychidae are discussed.

Keywords

Mesopsychidae, Mesopanorpodes, Mesopsyche, Permopsyche, Bittacopanorpa, Permian, Triassic, new taxa, revision

Introduction

Tillyard (1917b) described *Mesopanorpa wianamattensis* from the Middle Triassic Ashfield Formation of the Wianamatta Group in New South Wales as an aberrant Mecop-

tera and erected the family Mesopanorpidae. Later (Tillyard 1918) he changed the genus name to *Mesopanorpodes* to avoid homonymy with *Mesopanorpa* Handlirsch, 1906. Subsequently (Tillyard 1919b: 611–612) he decided that *Mesopanorpodes* was closely related to *Mesopsyche* and the allied genera *Aristopsyche*, *Triassopsyche*, and *Neuropsychyche* (the three latter have eventually been synonymized under *Mesopsyche* by Riek 1956), all described from the Upper Triassic Blackstone Formation, Queensland (Tillyard 1917a; Fig. 1E), and transferred *Mesopanorpodes* into the order Paratrichoptera.

Confusingly, this remark passed completely unnoticed by all the subsequent authors who discussed the composition and taxonomy of the Mesopanorpididae. Riek (1953) placed into Mesopanorpididae two new species of *Mesopanorpodes*, *M. belmontensis* and *M. robustus* (Fig. 1C–D), and the genus *Prochoristella* Riek, 1953 with six species from the Upper Permian of New South Wales (Belmont fossil beds). Since then, *Mesopanorpodes* and *Prochoristella* have been considered together either as forming a separate family Mesopanorpididae (Riek 1955, 1974, Jell and Duncan 1986, Willmann 1978, 1989, Carpenter 1992, Van Dijk and Geertsema 1999, Hong et al. 2002, Hong and Guo 2003, Hong 2007, Sun et al. 2007a, b), or as two closely related genera within Permochoristidae (Martynova 1962, Novokshonov 1997b, Novokshonov et al. 2004).

In fact, species of *Prochoristella* (with the possible exception of *P. belli* Riek, 1953, known only from a hindwing) display characters typical of Permochoristidae, that is, first of all, a deep fork on MA vein and an oblique base of CuA, either fused with MP for a distance, or forming cubito-median Y-vein. *Prochoristella* and *Mesopanorpodes* are similar only in the number of RS+MA and MP endings being reduced to four. However, this is characteristic of many independent lineages, e.g. Permotanyderidae + Liassophilidae, Nannochoeristidae, or Bittacidae, and cannot be accepted as a reliable apomorphy. I consider *Prochoristella*, including its possible junior synonyms (or at least closely related genera) *Afristella* Riek, 1974, *Mesotanyderus* Riek, 1955, and *Austrochoristella* Willmann, 1989, as belonging to Permochoristinae (Permochoristidae) and not related to *Mesopanorpodes*.

Equally unacceptable is the assignment to Mesopanorpididae of a number of species from the mid-Triassic Tongchuan Fm of Shaanxi Province, China, described by Hong You-Chong and co-authors (Hong et al. 2002, Hong and Guo 2003, Hong 2007). *Erdosia pectinata* Hong, Guo & Wang, 2002 can be placed with certainty into Parachoristidae, as indicated by the typical pectinate RS and 5- or 6-branched MP. “*Mesopanorpodes*” *shaanxiensis* Hong, Guo & Wang, 2002 is based on a highly incomplete hindwing and may belong to either Parachoristidae, Permochoristidae, or Mesopsychidae. The systematic position of *Ladinochorista lata* Hong, 2007 is uncertain because of the poor preservation of the holotype. Several other taxa described in Mesopanorpididae do not even belong to Mecoptera. *Triassochoristites jinsuoguanensis* Hong & Guo 2003 has already been recognized as a member of the dipteran family Vladipteridae (Blagoderov et al. 2007). *Forcinerva tongchuanensis* Hong and Guo 2003 belongs to the order Miomoptera (as determined by A.P. Rasnitsyn). *Allochorista erdosensis* Hong, 2007 and *Longifurcula hejiafangensis* Hong, 2007 cannot be attributed to any particular order based on the published photos and drawings. It should be noted that many descriptions of fossil insects from the Tongchuan Formation, and particularly Mecoptera, are based on inad-

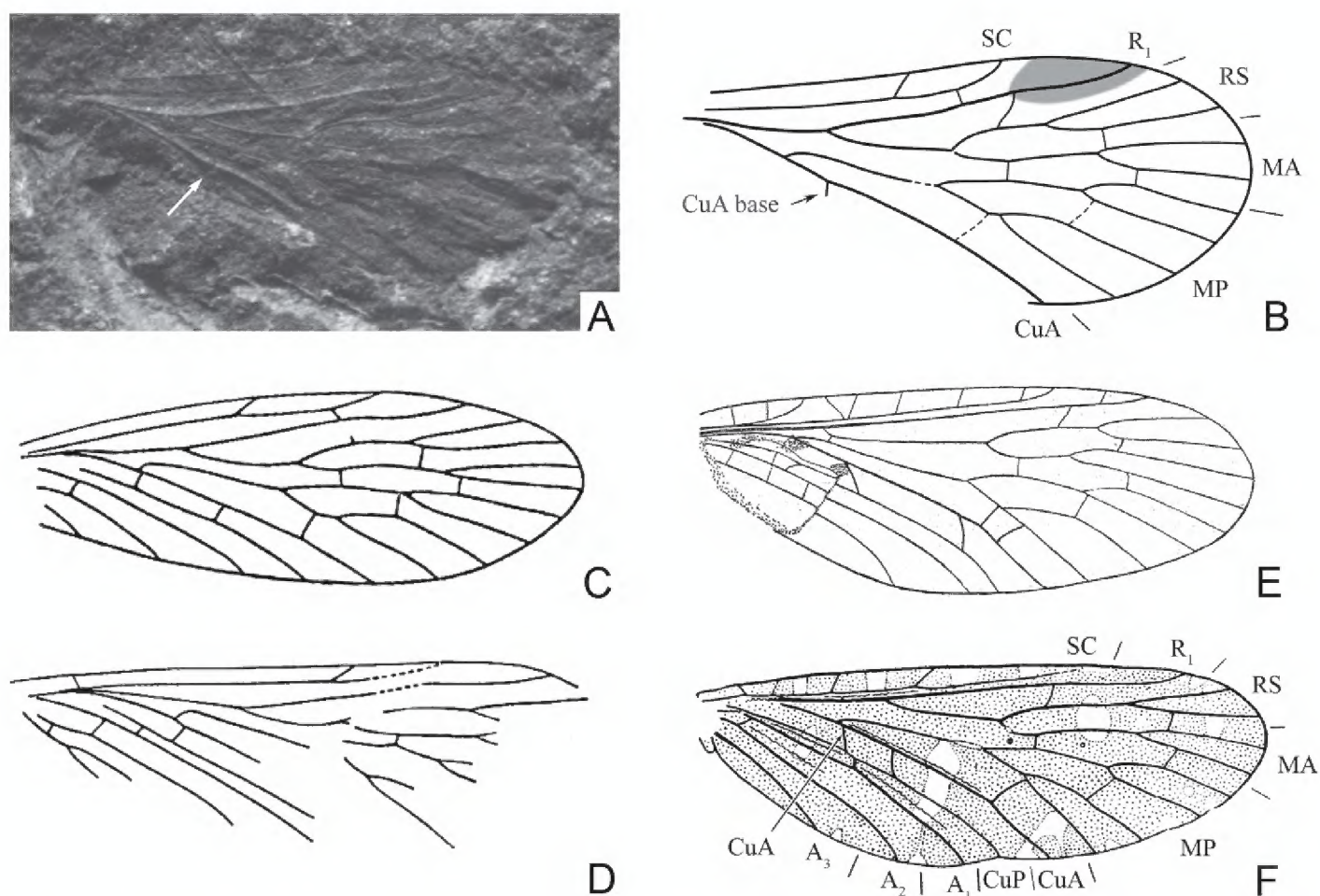


Figure 1. Wings of *Mesopanorpes* and *Mesopsyche*, for comparison **A** photograph of *Mesopanorpes wianamattensis* Tillyard (position of CuA base marked with arrow) **B** *Mesopanorpes wianamattensis*, line drawing (orig.) **C** *Mesopanorpes belmontensis*: from Riek (1953) **D** *Mesopanorpes robustus*: from Riek (1953) **E** *Mesopsyche triareolata* Tillyard (= *Aristopsyche superba* Tillyard): from Tillyard, 1919a **F** *Mesopsyche dobrokhotovae* Novokshonov, modified after Novokshonov (1997c). Not to scale.

equately preserved specimens and contain inaccurate drawings and fantastic venational interpretations, in which obvious artifacts are interpreted as characters of specific or even generic rank and hindwings are often misinterpreted as forewings. Thus, these taxa should be considered as of unknown systematic position until revised in detail.

The Jurassic genera *Itaphlebia* Sukatcheva, 1985 and *Chrysopanorpa* Ren, 1995 were originally placed in Mesopanorpididae as well. Novokshonov (1997a, b) synonymized these two genera and transferred them to Nannochoristidae. *Itaphlebia* appears to be the most common and widespread nannochoristid during the Jurassic. Its diagnosis, composition, and distribution, as well as the overall composition of the Mesozoic Nannochoristidae have been discussed recently by Liu et al. (2010).

Hong (2007) referred *Itaphlebia* again to Mesopanorpididae and described *I. tongchuanensis* from the Tongchuan Formation of Shaanxi. However, this species is not related to *Itaphlebia*, being instead rather similar to *Mesopsyche*, where it apparently belongs.

Stylopanorpes eurypterus, *Netropanorpes decorosus*, and *N. sentosus* Sun, Ren & Shih, 2007 (Sun et al. 2007b) from the mid-Jurassic Jiulongshan Formation of Inner Mongolia, China, originally placed in Mesopanorpididae, are venationally similar to the species of *Itaphlebia* occurring in the same deposits (Sun et al. 2007c, Liu et al. 2010) and belong to Nannochoristidae as well.

Mesopanorpodes mostovskii Novokshonov et al., 2004 from the basal Triassic of Northern Russia has been transferred to the related family Nedubroviidae (Bashkuev 2011).

Therefore, with the above-mentioned taxa discarded, Mesopanorpodidae remain composed of only three species of *Mesopanorpodes* from the Upper Permian and Middle Triassic of Australia. But are they actually congeneric?

Re-examination of available photographs of *M. wianamattensis* reveals that its CuA is distinctly bent distal to the origin of MP, and the base of CuA is shifted distad and inclined backwards, like in *Mesopsyche* (Fig. 1A–B). Thus, *Mesopanorpodes* appears venationally indistinguishable from *Mesopsyche*. Here I provisionally retain *Mesopanorpodes* as a separate genus until the complete revision of *Mesopsyche*. Unlike *M. wianamattensis* and *Mesopsyche*, both species described by Riek have the base of CuA short and transverse, with the intercubital space not expanded, which is presumed to be a plesiomorphic condition. These species are included here in the new genus *Permopsyche* gen. n.

In this paper, two new species of *Permopsyche*, *P. issadensis* sp. n. (type species) and *P. rasnitsyni* sp. n., are described from the Upper Permian of European Russia. These are the oldest currently known records of Mesopsychidae. The new material includes a number of well-preserved fore- and hindwings, which allow establishing yet another difference between *Permopsyche* and *Mesopsyche*, the position of the hindwing CuA vein with respect to the membrane. In *P. issadensis* CuA is concave (while the R_1 is convex), as is typical of Permochoristidae, while in *Mesopsyche* spp., including the Permian species, as well as the other Mesozoic mesopsychid genera, both CuA and R_1 are convex, like in most post-Paleozoic Mecoptera.

The earliest record of *Mesopsyche*, and the only one known so far to be definitely pre-Triassic, *Mesopsyche incompleta* sp. n., is described from the uppermost Permian of the European Russia.

Bittacopanorpa javorskii Zalesky, 1936 from the transitional Permian–Triassic sequence of the Kuznetsk Basin (Babiy Kamen' locality, Maltsevo Formation), known only from a wing base (Fig. 8G–H), originally placed in Neorthophlebiidae and tentatively transferred to Permotipulidae (Bechly and Schweigert 2000), can be identified as a hindwing with venation almost identical to that of the above-mentioned *Mesopsyche incompleta* sp. n. (Fig. 8B).

Material and methods

The study is based on examination of ca. 60 fossil specimens from the collection of Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). The holotype of *Bittacopanorpa javorskii* Zalesky is preserved in the collection of the Central Research Geological Prospecting Museum, Saint Petersburg (CRGPM).

Fifty-three isolated wings of *Permopsyche* were collected from a lens of fluvio-lacustrine deposits within the Sukhona River section, in Vologda Province, north-central Russia (Isady locality). It corresponds to the Kalikino Member of the Poldarsa Formation, and is dated the latest Severodvinian (correlated with the Lower Wuchiapingian: Golubev in press).

Five specimens of *Mesopsyche* were collected from the Balymotikha locality, an outcrop of lacustrine deposits of Vyazniki Permian–Triassic sequence, at the town of Vyazniki, Vladimir Province, central Russia. It is dated the latest Vyatkian (Late Changhsingian), somewhat below the Permian–Triassic boundary (Newell et al. 2010).

The fossils were examined with a Leica M165C stereomicroscope and photographed using an attached Leica DFC 425 digital camera. Images were digitally processed with Helicon Focus v. 5.1 and Adobe Photoshop CS3 graphic software. Line drawings were made using Inkscape v. 0.48 vector graphics editor.

On the line drawings the wings are oriented with their apices to the right, while some photographs are reversed left-right for better comparison.

The wing venation terminology follows Novokshonov (2002).

Systematic paleontology

Family Mesopsychidae Tillyard, 1917

<http://species-id.net/wiki/Mesopsychidae>

= Mesopanorpodidae Tillyard, 1918, syn. n.

Included genera. *Mesopsyche* Tillyard, 1917, *Mesopanorpodes* Tillyard, 1918, *Vitimopsyche* Novokshonov & Sukatsheva, 2001, *Baissopsyche* Novokshonov & Sukatsheva, 2001, *Lychnomesopsyche* Ren et al., 2009, *Permopsyche* Bashkuev, gen. n.

Remarks. The genus *Mesopanorpodes* is restricted here to its type species, *M. wianamattensis*. Though *Mesopanorpodes* appears venationally indistinguishable from *Mesopsyche*, it doesn't seem appropriate to synonymize these genera prior to the complete revision of the latter. The genus *Mesopsyche* (*sensu* Novokshonov 1997c, Novokshonov and Sukacheva 2001) includes apparently quite diverse insects and is quite loosely defined and likely heterogeneous, so its further dividing into several genera cannot be excluded.

Genus *Permopsyche* gen. n.

[urn:lsid:zoobank.org:act:57B809F6-634A-446C-AB88-79BE4E3E745C](http://species-id.net/wiki/Permopsyche)

<http://species-id.net/wiki/Permopsyche>

Mesopanorpodes: Riek, 1953, p. 70 (partim, quoad *M. belmontensis* and *M. robustus*).

Type species. *Permopsyche issadensis* sp. n.; Upper Permian, European Russia.

Etymology. From the Permian and Greek *psyche*, “soul” or “mind,” the word often used for devising names of delicately winged insects. Gender feminine.

Diagnosis. In forewing, SC long, bearing only inclined fore branch, connecting distally with R_1 by crossvein. Costal space narrow. Both RS and MA forks not longer than their stems. MP 4-branched. CuA base oblique to transverse, not distinctly in-

clined backwards; M_5 present or lost. Anal area not expanded. Crossveins not numerous. In hindwing, CuP concave with respect to membrane (in contrast to convex R_1).

Comparison. Differs from the closest genus *Mesopsyche* by the base of CuA being oblique to transverse (not inclined backwards), costal space narrower, and hindwing CuP concave with respect to membrane.

Composition. In addition to the type species, from the same locality, *P. rasnitsyni* sp. n.; and from the Upper Permian of Australia, *P. belmontensis* (Riek, 1953) comb. n. and *P. robustus* (Riek, 1953) comb. n.

Remarks. The assumption that one of the key characters, the position of hindwing CuP with respect to the membrane, known in the type species only, is shared by the other species is tentative and requires further verification.

***Permopsyche issadensis* sp. n.**

urn:lsid:zoobank.org:act:FBCADCA5-E2B6-4D4E-B044-6DE29496AAFD

http://species-id.net/wiki/Permopsyche_issadensis

Figs 2–4, 6

Etymology. From the Isady locality.

Holotype. PIN, no. 3840/336, well-preserved forewing (part and counterpart).

Paratypes. 21 forewings (see Table 1) and 6 hindwings: PIN, no. 3840/725, 1381–1383, 1385, 1389a. Additionally, 8 forewings and 10 hindwings incomplete or poorly preserved, excluded from the type series.

Locality and horizon. Isady locality, Vologda Province, North European Russia; Poldarsa Formation, uppermost Severodvinian (Lower Wuchiapingian), Upper Permian.

Diagnosis. Differs from *P. belmontensis* by wing shape, with anterior margin straight and posterior apical margin tending to oblique, different crossveins arrangement, and strongly unsclerotized MP stem. Differs from *P. robustus* by branch of SC located more basally and A_3 simple. Additionally differs from both species by considerably smaller size.

Description. Forewing. Moderately broad (length/width ratio 2.3–2.9:1); anterior margin nearly straight, slightly convex basally; apex obtuse to rounded. SC long, reaching or almost reaching basal margin of pterostigma; SC branch approximately at middle of RS+MA stem (somewhat variable in paratypes). Pterostigma distinct, widened, with oblique basal margin. R_1 simple, gently bending posteriad at pterostigma. RS and MA forks equally short, approximately as long as their stems. Nodal line distinct, arched, running from tip of SC to hind margin at apex of CuA. Thyridium present as unsclerotized section on MP stem spanning from approximately 1/3–1/2 of its length down to fork, accompanied by desclerotized spot at point of branching of RS and MA (“thyridulum”, the term introduced by A.P. Rasnitsyn in Ren et al. 2009). Connection between CuA and MP variable (Fig. 4; see also Remarks), from joined at one point (X-junction), with CuA base oblique and M_5 lost, to forming well-developed cubito-median Y-vein with almost equal arms at obtuse angle, with CuA base transverse and M_5 quite long. cua-cup crossvein transverse. Three simple anal veins. Crossveins not nu-

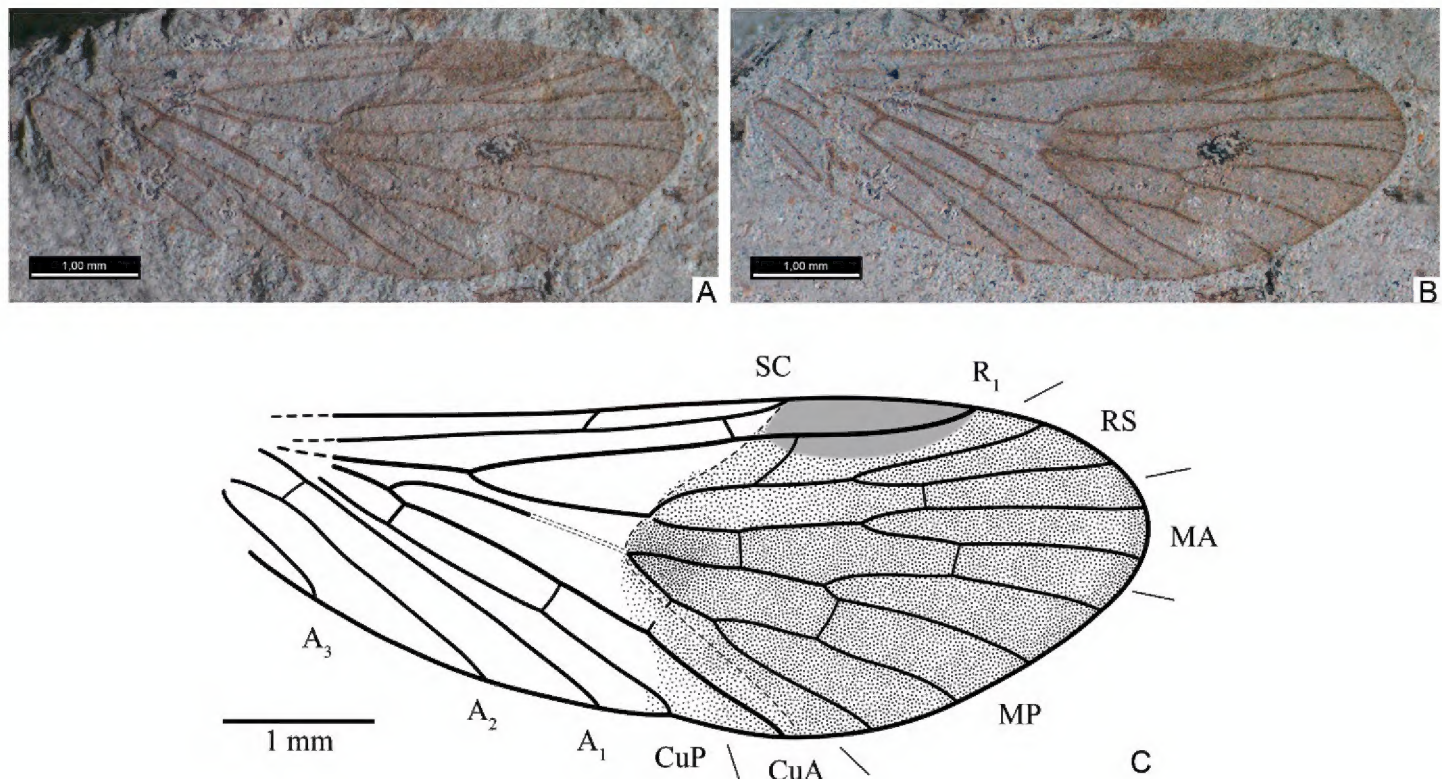


Figure 2. *Permopsyche issadensis* gen. et sp. n. **A–B** photographs of the holotype, under different illumination **C** line drawing of holotype.

merous, mainly distinct or slightly weakened, forming rather stable pattern: one long, oblique, sigmoidally curved r_1 -rs crossvein; four crossveins between RS, MA, and MP branches; mp-cua and cua-cup crossveins of standard position; cup- a_1 and a_1 - a_2 located stepwise along with the base of CuA; occasionally, a_2 - a_3 present. Wing membrane darkened in distal wing half, restricted by nodal line, with saturated patch at center of wing.

Hindwing. Both venation scheme and coloration similar to those in forewing, adjusted for general difference between fore- and hindwings typical of Mecoptera. SC short, reaching wing midlength, variably forking apically (Fig. 6). Pterostigma distinct. R_1 with inclined branch in pterostigmal area. A_1 separating from CuP relatively closely to base.

Measurements (mm). Forewing length, 4.25–6.35, width, ca. 1.5–2.5; hindwing length, 3.9–5.5, width, 1.5–2.25.

Remarks and discussion. In *P. issadensis* the wing size varies conspicuously. As shown in the size distribution diagram for forewings (Fig. 5; Table 1), the presence of Y-vein and the transverse (rather than oblique) shape of CuA base (hollow squares *vs* filled squares) both correlate with the increased wing size (irrespective of the length/width ratio). However, the size distributions of the two morphotypes overlap broadly. The two wing morphotypes may represent sexual dimorphism. Alternatively, they can be attributed to slight differences in flight mechanics depending on the body size. The distinctive and uniform wing color pattern makes it unlikely that the morphotypes represent two closely related species.

The nodal line (the line of wing flexion) in the forewing of the new species is essentially similar to that of both *Mesopsyche* (Novokshonov 1997c) and the recent *Panorpa* (Ennos and Wootton 1989), suggesting a similarity between flight mechanics of Mesopsychidae and Panorpidae.

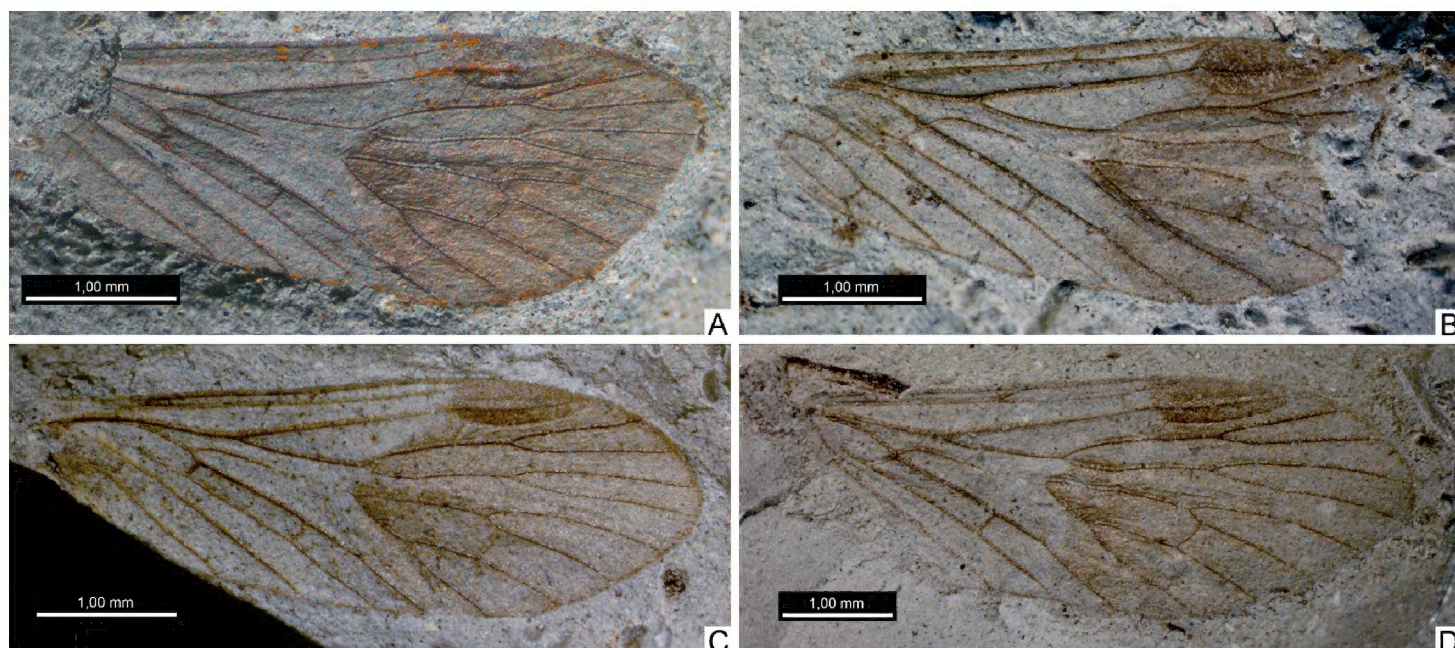


Figure 3. Photographs of forewings of *Permopsysche issadensis* gen. et sp. n. **A** paratype PIN, no. 3840/717; **B** paratype PIN, no. 3840/1354 **C** paratype PIN, no. 3840/1355 **D** paratype PIN, no. 3840/1357. All except **D** reversed left-right.

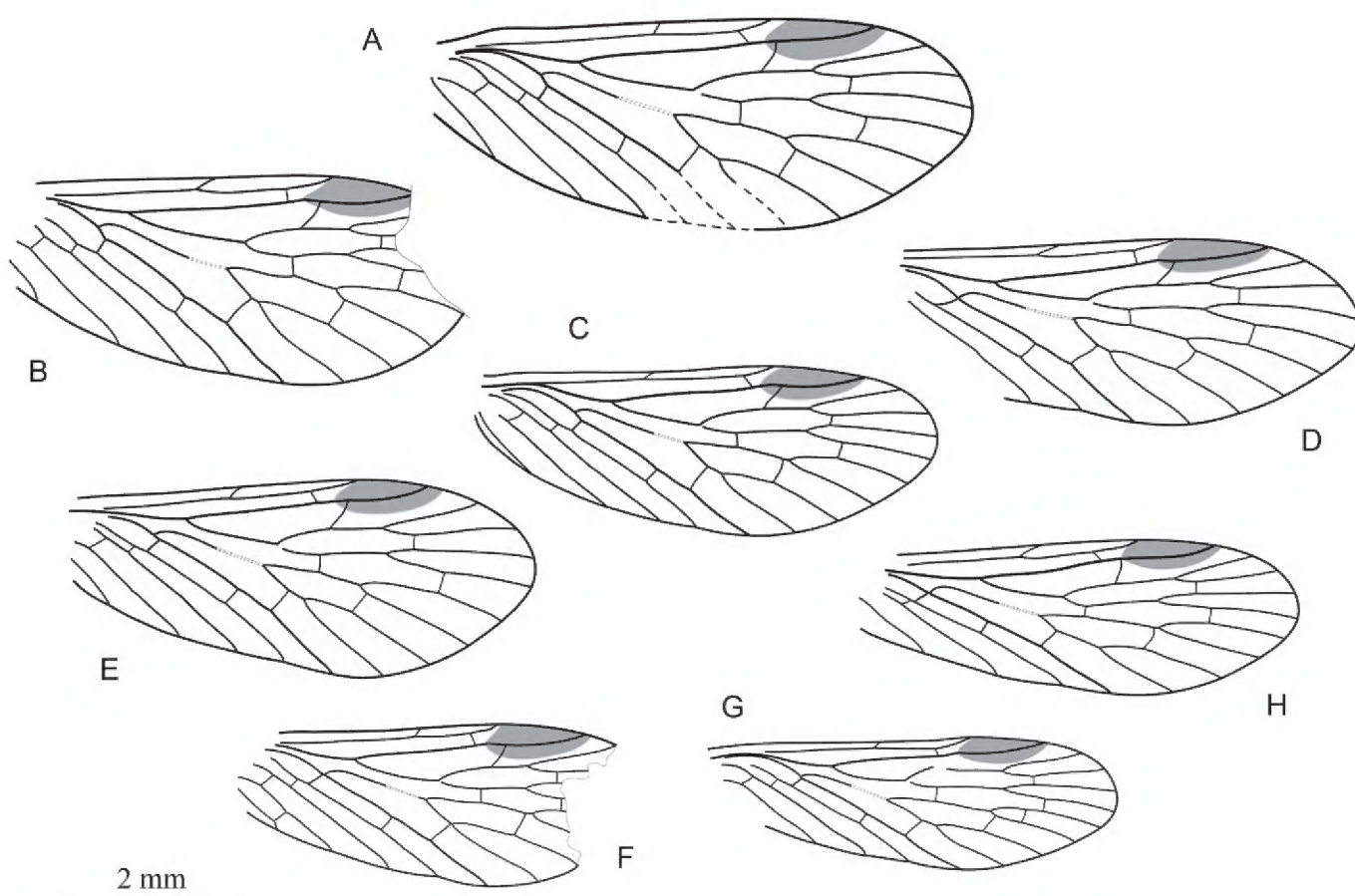


Figure 4. Line drawings of paratypes of *Permopsysche issadensis* gen. et sp. n. showing the variability of venation and wing size **A** PIN, no. 3840/718 **B** PIN, no. 3840/719 **C** PIN, no. 3840/105 **D** PIN, no. 3840/1357 **E** PIN, no. 3840/1352 **F** PIN, no. 3840/1354 **G** PIN, no. 3840/728 **H** PIN, no. 3840/729. All to the same scale.

Hindwings of *Permopsysche* are almost as abundant at Isady as the forewings. All the hindwings examined, as far as their preservation allows to tell, have the set of characters (including coloration) diagnostic of the forewings of *P. issadensis* and can be confidently referred to the same species.

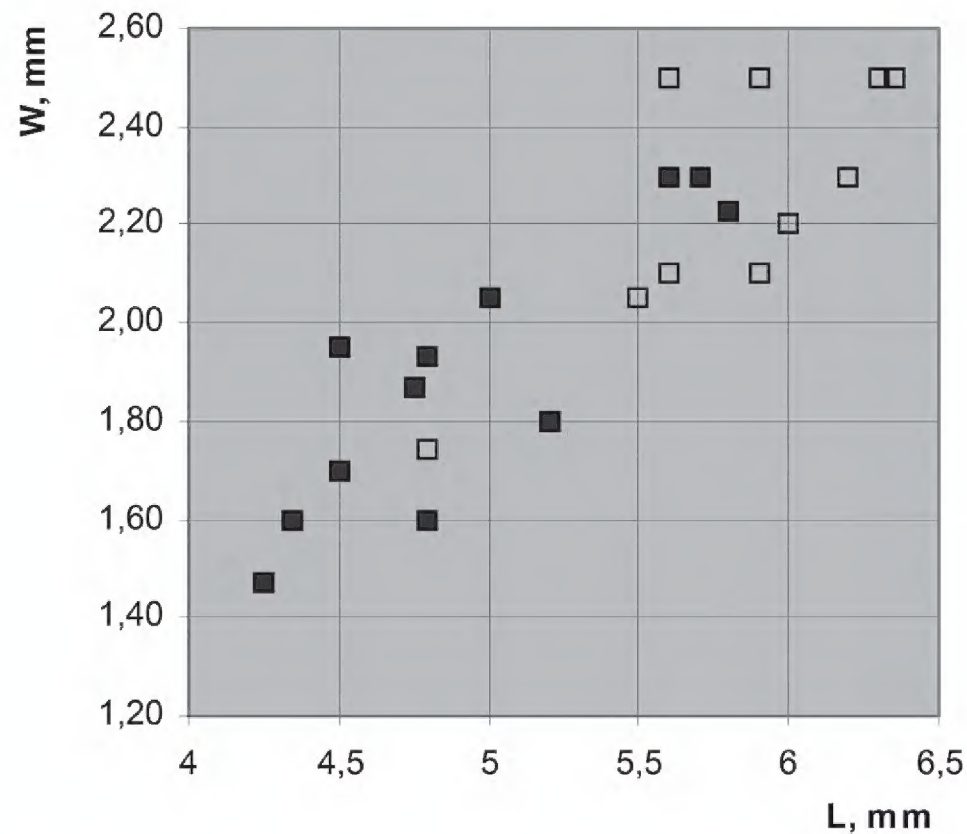


Figure 5. Correlation between wing size and structure of connection between CuA and MP in *Permopsysche issadensis*, based on Table 1; see text for explanation.

Table 1. Forewing sizes of *Permopsysche issadensis* gen. et sp. n. Some measurements are acceptably approximate due to restoration of wing base and/or apex.

PIN, no. 3840/...	Length	Width	L:W	CuA/MP fusion
730	4.25	1.47	2.89	■
1362	4.35	1.6	2.72	■
1360	4.5	1.7	2.65	■
723	4.5	1.95	2.31	■
1367	4.75	1.87	2.54	■
728	4.8	1.6	3.00	■
1355	4.8	1.74	2.76	□
1354	4.8	1.93	2.49	■
1359	5.0	2.05	2.44	■
729	5.2	1.8	2.89	■
105	5.5	2.05	2.68	□
1349	5.6	2.1	2.67	□
1352	5.6	2.3	2.43	■
719	5.6	2.5	2.24	□
1358	5.7	2.3	2.48	■
1357	5.8	2.23	2.60	■
1353	5.9	2.1	2.81	□
1350	5.9	2.5	2.36	□
1366	6.0	2.2	2.73	□
336	6.2	2.3	2.70	□
717	6.3	2.5	2.52	□
718	6.35	2.5	2.54	□

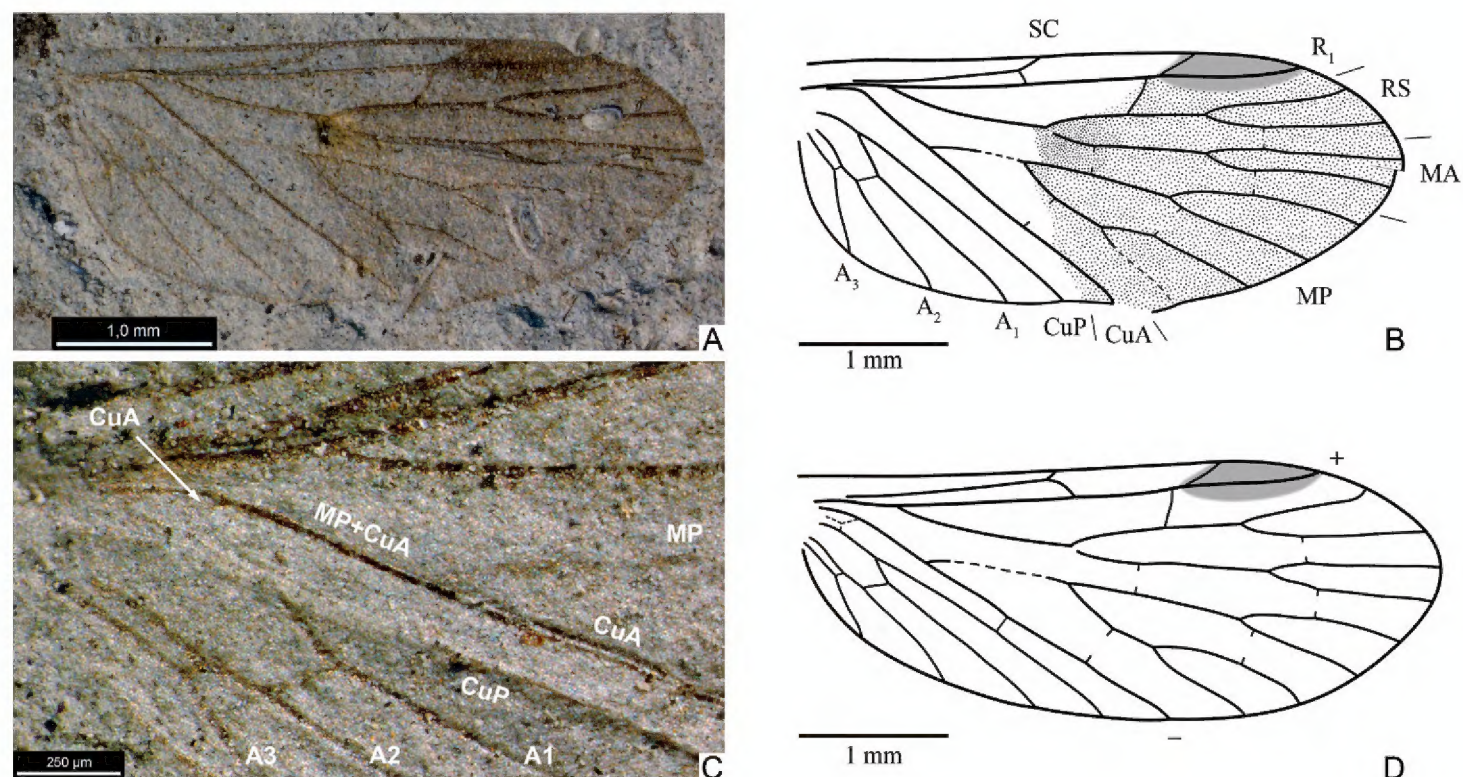


Figure 6. Hindwings of *Permopsysche issadensis* gen. et sp. n. **A–B** paratype PIN, no. 3840/1381, photograph and line drawing **C–D** paratype PIN, no. 3840/1382 **C** details of cubito-anal structure **D** line drawing of hindwing **A, C** reversed left-right.

***Permopsysche rasnitsyni* sp. n.**

urn:lsid:zoobank.org:act:E74CC301-D5B9-4093-9194-BCE6B1C852D2

http://species-id.net/wiki/Permopsysche_rasnitsyni

Fig. 7A–D

Etymology. In honor of an outstanding paleoentomologist, Prof. Dr. Alexandr Rasnitsyn.

Holotype. PIN, no. 3840/1351, well-preserved forewing (part and counterpart), with apex missing.

Paratypes. PIN, no. 3840/733, 1363, 1371, incomplete forewings.

Locality and horizon. Isady locality, Vologda Province, North European Russia; Poldarsa Formation, uppermost Severodvinian (Lower Wuchiapingian), Upper Permian.

Diagnosis. Similar to *P. issadensis* in general venation scheme, but of larger size, with MA fork shortened, intercubital space widened, and wing membrane almost uncolored.

Description. Forewing length/width ratio about 2.8–3:1; anterior margin nearly straight; apex obtuse to rounded. Costal space very narrow along its entire length. MA fork distinctly shorter than RS fork. MP unsclerotized for more than 1/2 of its length. CuA base long, nearly transverse, M_5 present or lost. Intercubital space rather expanded. Wing membrane mostly uncolored, with small diffuse dark patch at center of wing.

Measurements (mm). Holotype length, as preserved, 6.7, width, 2.5; paratypes lengths, ca. 7.0–8.5, width unmeasurable due to widthwise deformation.

***Permopsyche* sp.**

Fig. 7E–F

Material. PIN, no. 3840/1556, well-preserved forewing (part and counterpart).

The wing is 6 mm long, 2.1 mm wide, subtriangular, with anal area narrowed and posterior apical margin slightly oblique; MA forking before RS. The wing is entirely uncolored (neither part, nor counterpart showing any trace of coloration). The specimen may either be an aberrant specimen of *Permopsyche issadensis*, or represent a different species, but describing a separate species based on a single wing does not seem well justified.

Genus *Mesopsyche* Tillyard, 1917

<http://species-id.net/wiki/Mesopsyche>

Triassopsyche Tillyard, 1917: Riek 1956, p. 100.

Aristopsyche Tillyard, 1919: Riek 1956, p. 100.

Neuropsychyche Tillyard, 1919: Riek 1956, p. 100.

Mesoses Riek, 1976: Novokshonov and Sukatcheva 2001, p. 71.

Bittacopanorpa Zalessky, 1935, syn. n.

Itaphlebia Hong, 2007, syn. n. (partim, quoad *I. tongchuanensis*)

Type species. *Mesopsyche triareolata* Tillyard, 1917; Upper Triassic, Australia.

Diagnosis. Forewing relatively broad. SC rather long, with single or multiple fore branches. Costal space typically expanded. Both RS and MA forks not longer than their stems. MP 4-branched. CuA base from transverse to distinctly inclined backwards, usually situated much more distally than MP origin. Crossvein cua-cup of same inclination as CuA base. Intercubital space rather expanded. Crossveins not numerous, their arrangement rather stable. In hindwing, CuP convex with respect to membrane; fused with A_1 very close to base.

Comparison. Differs from *Permopsyche* by the base of CuA being inclined backwards, costal space widened, and hindwing CuP convex.

Composition. In addition to the type species, from the beds near the Permian–Triassic boundary of Kuznetsk Basin, *M. javorskii* (Zalessky, 1935) comb. n.; from the Middle Triassic of China, *M. tongchuanensis* (Hong, 2007) comb. n.; from the Middle–Upper Triassic Madygen Formation of Kyrgyzstan, *M. shcherbakovi*, *M. justa*, *M. ordinata*, *M. tortiva*, and *M. gentica* (Novokshonov 1997c, Novokshonov and Sukatcheva 2001); from the Upper Triassic of South Africa, *M. optata* (Riek, 1976), *M. magna* (Riek, 1976); from the Upper Triassic of Ukraine, *M. dobrokhotovae* (Novokshonov 1997c).

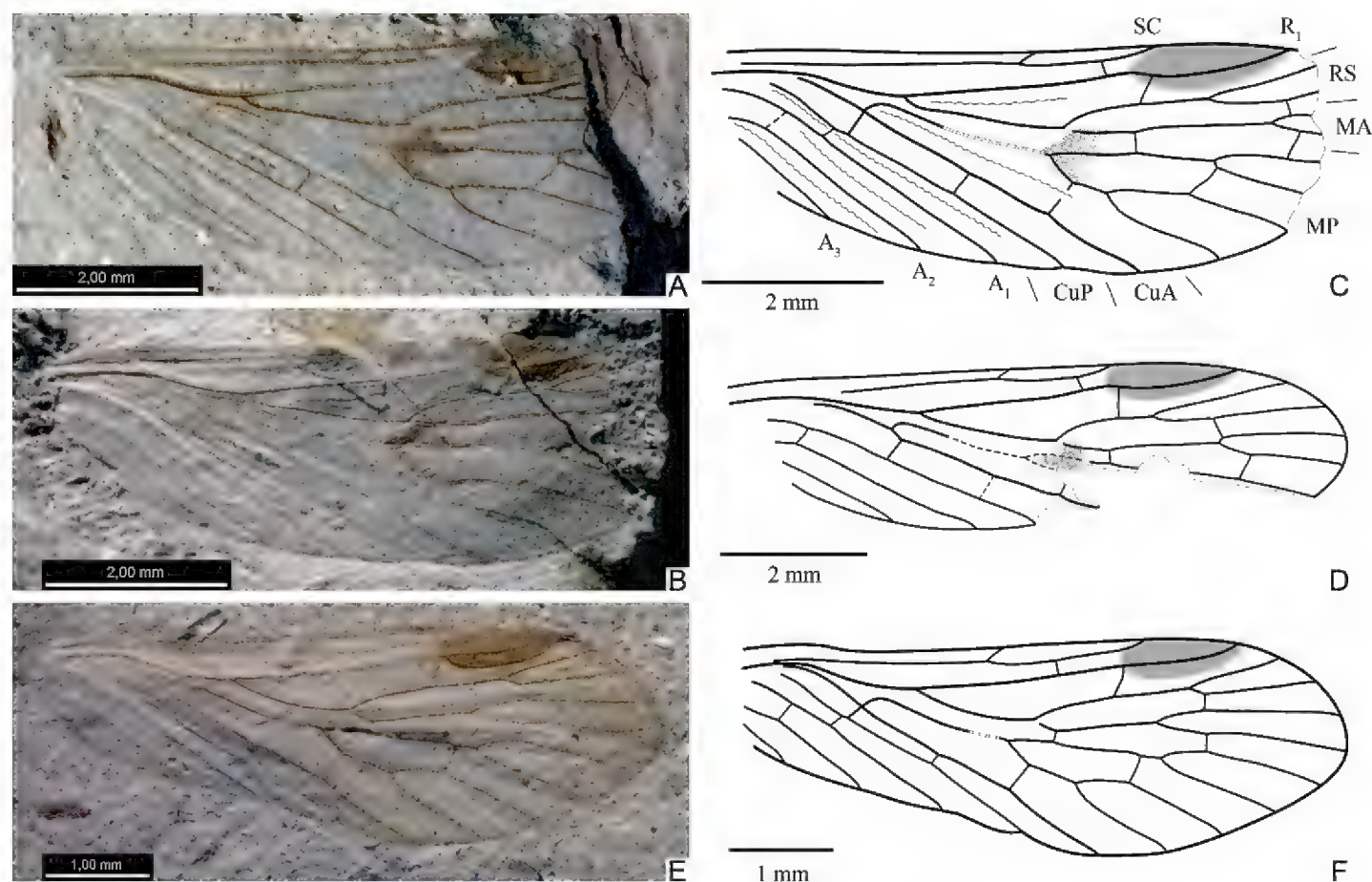


Figure 7. **A–D** forewings of *Permopsysche rasnitsyni* gen. et sp. n. **A–B** photograph of holotype, PIN, no. 3840/1351, part and counterpart **C** line drawing of holotype, PIN, no. 3840/1351 **D** line drawing of paratype, PIN, no. 3840/1363 **E–F** *Permopsysche* sp., photograph and line drawing of specimen PIN, no. 3840/1556.

***Mesopsysche incompleta* sp. n.**

urn:lsid:zoobank.org:act:FC61FFCE-6E4D-401F-BD62-227A6E376D1B

http://species-id.net/wiki/Mesopsysche_incompleta

Fig. 8

Etymology. Latin *incompletus*, “incomplete”.

Holotype. PIN, no. 5103/286, hindwing (part and counterpart), with cubito-anal area missing.

Paratypes. PIN, no. 5103/122, incomplete forewing (basal half only), part and counterpart; PIN, no. 5103/123, incomplete forewing (anterior half only, with apex, basal and posterior parts missing), part and counterpart. In addition, two forewing fragments apparently belonging to the same species.

Locality and horizon. Balymotikha locality, Vyazniki town, Vladimir Province, Central European Russia; uppermost Vyatkian (Upper Changhsingian), Upper Permian.

Description. Forewing. Anterior margin slightly convex. Costal space somewhat wider than subcostal one. Pterostigma distinct, lanceolate. SC not reaching the pterostigma, bearing one oblique distal branch; connected distally with R_1 by short transverse crossvein. R_1 sharply curved posteriad at origin of weak distal branch in pterostig-

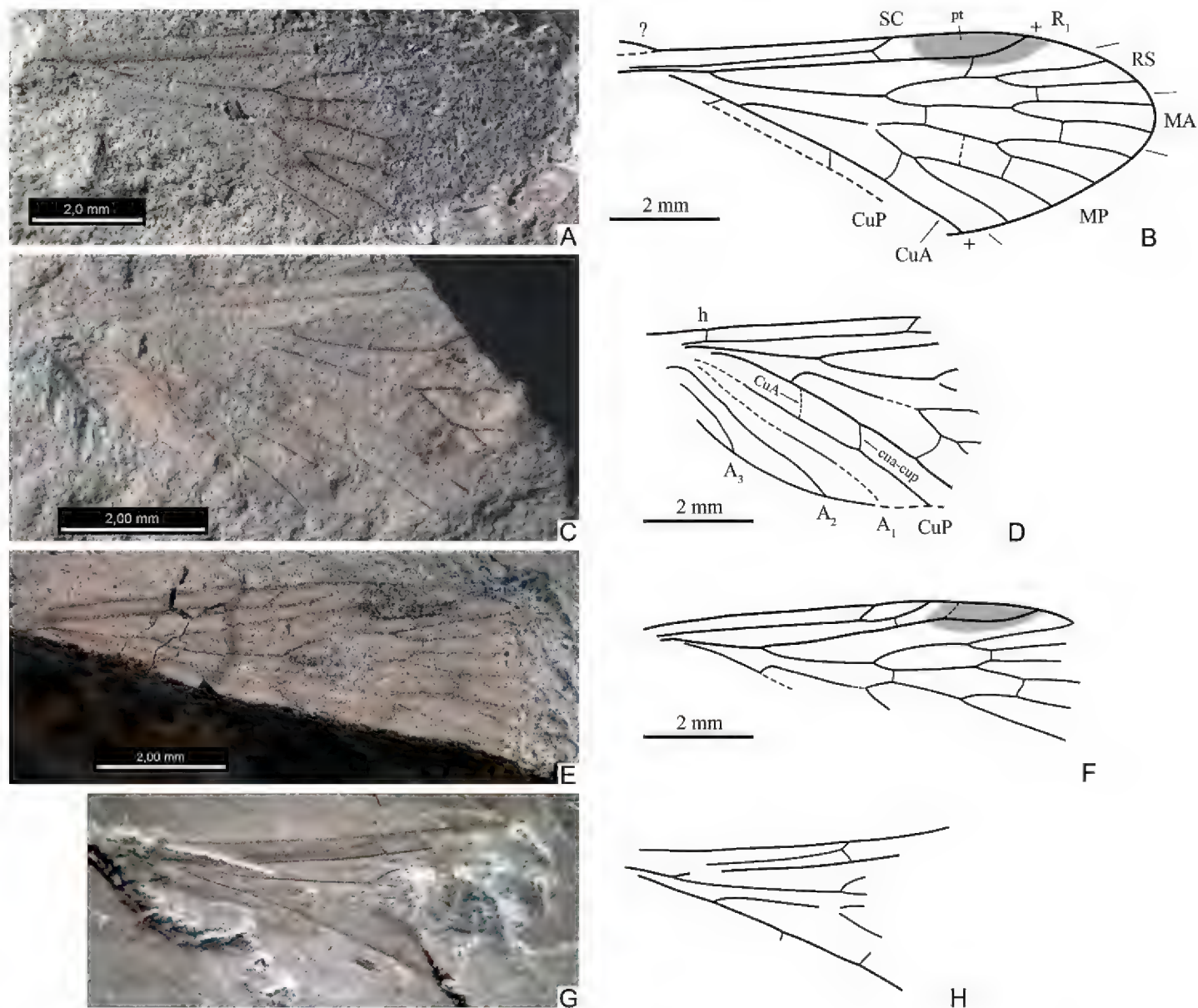


Figure 8. **A–F**, wings of *Mesopsyche incompleta* sp. n. **A–B** holotype PIN, no. 5103/286, hindwing, photograph and line drawing **C–D** paratype PIN, no. 5103/122, forewing, photograph and line drawing **E–F** paratype PIN, no. 5103/123, forewing, photograph and line drawing **G–H** *Mesopsyche javorskii* (Zalessky) comb. n., holotype hindwing, photograph (by D. Shcherbakov) and line drawing (orig.), not to scale **A, C, G** reversed left-right.

mal area. RS forking somewhat before than MA. Thyridium at MP stem before fork. CuA base obscure, presumably curved backwards and located somewhat distal to M_5 . Crossvein cua-cup slightly sigmoid, distinctly curved backwards. Crossvein pattern typical of genus. Color pattern in form of sparse dark spots, mostly around crossveins.

Hindwing venation and coloration similar to those in forewing. SC slightly shortened, reaching level of RS+MA bifurcation, somewhat beyond wing midlength, forking apically. Pterostigma distinct. R_1 nearly straight, turning apically towards anterior margin. R_1 branch obscure. CuA distinctly convex along the whole length.

Measurements (mm). hindwing length of holotype, 9.8; forewing length of paratype PIN, no. 5103/122, 6.1, as preserved; paratype PIN, no. 5103/123, 7.9, as preserved.

Comparison. The new species substantially differs from others by SC with a single, distally located fore branch.

Discussion

The systematic position of Mesopsychidae and the entire “suborder” Paratrichoptera was discussed by Novokshonov and Sukatcheva (2001). Recent studies of complete mesopsychid fossils from the Middle Jurassic and Lower Cretaceous of China revealed the long siphonate mouthparts indicating fluid feeding on reproductive organs of gymnosperm plants (Ren et al. 2009, 2010). Mesopsychidae, together with mid-Mesozoic Aneuretopsychnidae, Pseudopolycentropodidae, and now the Late Permian to Early Triassic Nedubroviidae (Bashkuev 2011), form a distinct long-proboscid clade within Mecoptera, the Aneuretopsychnina.

The finds described herein reveal main trends in the evolution of Mesopsychidae after their separation from the permochoristid-like ancestor. These are:

- Change in the forewing CuA base inclination and position: from proximal and inclined forwards (typical of Permochoristidae) to inclined backwards, and probably also shifted distad.
- Change in position of the hindwing CuA: from concave (*Permopsyche*) to convex (most Mesopsychidae).
- Loss of fusion of CuP and A₁ veins in the hindwing: from quite basally fused in *Permopsyche*, through a rudimentary basal fusion in *Mesopsyche* (as indicated by Novokshonov (1997c) in *M. shcherbakovi*), to becoming secondary free along their whole length in the mid-Jurassic and early Cretaceous genera.
- Increase in the average wing size, from 5–6 mm in the Late Permian to 20–30 mm since the Late Triassic.

The Permian Mesopsychidae occurred together with Nedubroviidae (in Isady, Ballymotikha, and probably Belmont; Bashkuev 2011), which already have typical long siphonate mouthparts, and the possession of those in early mesopsychids (and even in the ancestral permochoristid lineage) can be assumed as well.

New finds also cast light on the stratigraphic distribution of the Aneuretopsychnina scorpionflies, which appear to be the most common group of Mecoptera during the latest Permian – early Middle Triassic time interval (viz. Mesopsychidae, Nedubroviidae, and later also Pseudopolycentropodidae). They initially replaced Permochoristidae in the end of Permian, and were in turn progressively supplanted during the Triassic – Early Jurassic by Parachoristidae and Orthophlebiidae, which gave rise to the modern mecopteran lineages. In the mid-Jurassic – Lower Cretaceous insect assemblages, Aneuretopsychnina scorpionflies are rather rarely found, constituting only a minor component of the mecopteran faunas.

Acknowledgements

I am grateful to Prof. Alexandr Rasnitsyn and Dr Dmitry Shcherbakov for valuable comments and discussions, to Dr Louis A. Somma for reviewing the paper and im-

portant remarks, to Dr Yong Yi Zhen who kindly provided the photographs of *Mesopanorpodes* from the collection of the Australian Museum, Sydney, and to Dr Roman Rakitov for improving the English of manuscript. The research was supported by the Russian Foundation for Basic Research, projects 09-04-01241 and 10-04-01713, and by the Program 15 of the Presidium of the Russian Academy of Sciences “The Origin of the Biosphere and Evolution of the Geo-Biosystems”.

References

- Bashkuev AS (2011) Nedubroviidae, a new family of Mecoptera: the first Paleozoic long-proboscoid scorpionflies. *Zootaxa* 2895: 47–57.
- Bechly G, Schweigert G (2000) The first fossil hanging flies (Insecta: Mecoptera: Raptipedia: Cimbrophlebiidae and Bittacidae) from the limestones of Solnhofen and Nusplingen (Upper Jurassic, Germany). *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 287: 1–18.
- Blagoderov V, Grimaldi DA, Fraser NC (2007) How time flies for flies: diverse Diptera from the Triassic of Virginia and early radiation of the order. *American Museum Novitates* 3572: 1–39. doi: 10.1206/0003-0082(2007)509[1:HTFFFD]2.0.CO;2
- Carpenter FM (1992) Order Mecoptera Packard, 1886. In: *Treatise on Invertebrate Paleontology*. Pt. R: Arthropoda 4. Vol. 4: Superclass Hexapoda. Geological Society of America, Boulder, Colorado and University of Kansas, Lawrence, Kansas, 380–395.
- Ennos RA, Wootton RJ (1989) Functional wing morphology and aerodynamics of *Panorpa germanica* (Insecta: Mecoptera). *Journal of Experimental Biology* 143: 267–284.
- Golubev VK (in press) Upper Permian fossil remains locality Mutovino (=Isady) from the river Sukhona (Vologda region): geology and paleontology. *Paleontological Journal*.
- Handlirsch A (1906) *Die fossilen Insekten und die Phylogenie der rezenten Formen: Ein Handbuch für Paläontologen und Zoologen*. Leipzig, 1430 pp.
- Hong Y-C (2007) Midtriassic new genera and species of Mesopanorpodidae (Insecta: Mecoptera) from Shaanxi, China. *Acta Zootaxonomica Sinica* 32: 261–267.
- Hong Y-C, Guo X-R (2003) Two new Middle Triassic genera and species of Mesopanorpodidae from Shaanxi (Insecta, Mecoptera). *Acta Zootaxonomica Sinica* 28: 716–720.
- Hong Y-C, Guo X-R, Wang W-L (2002) Middle Triassic New Fossils of Mesopanorpodidae (Insecta: Mecoptera) from Tongchuan, Shaanxi Province, China. *Acta Zootaxonomica Sinica* 27: 278–283.
- Jell PA, Duncan PM (1986) Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoirs of the Association of Australasian Palaeontologists* 3: 111–205.
- Liu N, Zhao Y, Ren D (2010) Two new fossil species of *Itaphlebia* (Mecoptera: Nannochoristidae) from Jiulongshan Formation, Inner Mongolia, China. *Zootaxa* 2420: 37–45.
- Martynova OM (1962) Order Mecoptera: Scorpionflies. In: Rohdendorf BB (Ed) *Fundamentals of Paleontology*. Vol. 9, Arthropoda, Tracheata, Chelicerata. Moscow, 283–294. [in Russian; translated into English: (1991) Amerind Publishing, New Delhi, 405–424]

- Newell AJ, Sennikov AG, Benton MJ, Molostovskaya II, Golubev VK, Minikh AV, Minikh MG (2010) Disruption of playa-lacustrine depositional systems at the Permo–Triassic boundary: evidence from Vyazniki and Gorokhovets on the Russian Platform. *Journal of the Geological Society* 167: 695–716. doi: 10.1144/0016-76492009-103
- Novokshonov VG (1997a) New and little known Mesozoic Nannochoristidae (Insecta: Mecoptera). *Vestnik Permskogo Universiteta (Biologiya)* 4: 126–135. [in Russian, with English abstract]
- Novokshonov VG (1997b) Early Evolution of the Scorpionflies (Insecta: Panorpidia). Nauka, Moscow, 140 pp. [in Russian]
- Novokshonov VG (1997c) Some Mesozoic scorpionflies (Insecta: Panorpidia = Mecoptera) of the families Mesopsychidae, Pseudopolycentropodidae, Bittacidae, and Permochoristidae. *Paleontological Journal* 31: 65–71.
- Novokshonov VG, Sukatcheva ID (2001) Fossil scorpionflies of the “suborder” Paratrachoptera (Insecta: Mecoptera). *Paleontological Journal* 35: 173–182.
- Novokshonov VG (2002) Order Panorpidia Latreille, 1802. In: Rasnitsyn AP and Quicke DLJ (eds.), *History of Insects*. Kluwer Academic Press, Dordrecht, 194–199.
- Novokshonov VG, Sukacheva ID, Aristov DS (2004) An Early Triassic scorpionfly (Panorpidia = Mecoptera) of the Vologda Region. *Paleontological Journal* 38 (Suppl. 2): S214–S215.
- Ren D, Labandeira CC, Santiago-Blay JA, Rasnitsyn AP, Shih C-K, Bashkuev A, Logan MAV, Hotton CL, Dilcher DL (2009) A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. *Science* 326: 840–847. doi: 10.1126/science.1178338
- Ren D, Labandeira CC, Shih C-K (2010) New Mesozoic Mesopsychidae (Mecoptera) from northeastern China. *Acta Geologica Sinica (English edition)* 84: 720–731. doi: 10.1111/j.1755-6724.2010.00244.x
- Riek EF (1953) Fossil mecopteroid insects from the Upper Permian of New South Wales. *Records of the Australian Museum* 23: 55–87. doi: 10.3853/j.0067-1975.23.1953.621
- Riek EF (1955) Fossil insects from the Triassic beds at Mt. Crosby, Queensland. *Australian Journal of Zoology* 3: 654–691. doi: 10.1071/ZO9550654
- Riek EF (1956) A re-examination of the mecopteroid and orthopteroid fossils (Insecta) from the Triassic beds at Denmark Hill, Queensland, with description of further specimens. *Australian Journal of Zoology* 4: 98–110. doi: 10.1071/ZO9560098
- Riek EF (1974) Upper Triassic insects from the Molteno “Formation”, South Africa. *Palaeontologia Africana* 17: 19–31.
- Riek EF (1976) A new collection of insects from the Upper Triassic of South Africa. *Annals of the Natal Museum* 22: 791–820.
- Sun J-H, Ren D, Huang J-D (2007a) Current knowledge of research on Mecoptera fossils in China. *Acta Zootaxonomica Sinica* 32: 881–889. [in Chinese, with English abstract]
- Sun J-H, Ren D, Shih Ch-K (2007b) Middle Jurassic Mesopanorpididae from Daohugou, Inner Mongolia, China (Insecta, Mecoptera). *Acta Zootaxonomica Sinica* 32: 865–874.
- Sun J-H, Ren D, Shih Ch-K (2007c) Middle Jurassic Nannochoristidae fossils from Daohugou, Inner Mongolia in China (Insecta, Mecoptera). *Acta Zootaxonomica Sinica* 32: 405–411.

- Tillyard RJ (1917a) Mesozoic insects of Queensland. No. 1. Planipennia, Trichoptera, and the new order Protomecoptera. *Proceedings of the Linnean Society of New South Wales* 42: 175–200.
- Tillyard RJ (1917b) Permian and Triassic insects from New South Wales in the collection of Mr. J. Mitchell. *Proceedings of the Linnean Society of New South Wales* 42: 720–756.
- Tillyard RJ (1918) Mesozoic insects of Queensland. No. 3. Odonata and Protodonata. *Proceedings of the Linnean Society of New South Wales* 43: 417–436.
- Tillyard RJ (1919a) Mesozoic insects of Queensland. No. 5. Mecoptera, the new order Paratri-choptera, and additions to Planipennia. *Proceedings of the Linnean Society of New South Wales* 44: 194–212.
- Tillyard RJ (1919b) The panorpoid complex. Pt. 3: The wing venation. *Proceedings of the Linnean Society of New South Wales* 44: 533–718.
- Van Dijk DE, Geertsema H (1999) Permian Insects from the Beaufort Group of Natal, South Africa. *Annals of the Natal Museum* 40: 137–171.
- Willmann R (1978) Mecoptera (Insecta, Holometabola). In: *Fossilium Catalogus, Animalia*. Pars 124. W. Junk, The Hague, 1–139.
- Willmann R (1989) Evolution und phylogenetisches System der Mecoptera (Insecta: Holometabola). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 544: 1–153.
- Zalessky G (1936) Sur deux restes d'insectes fossiles provenant du bassin de Kousnetzky et sur l'âge géologique des dépôts qui les renferment. *Bulletin de la Société géologique de France* 5: 687–695.